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John Timothy Inglis
University of British Columbia

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THE ROLE OF CUTANEOUS RECEPTORS IN THE FOOT

J. Timothy Inglis, Paul M. Kennedy, Cari Wells, and Romeo Chua*

ABSTRACT

Cutaneous receptors in the foot sole appear to contribute to the control of human stance and locomotion. Two approaches were undertaken to establish the characteristics of the receptors in the sole. Psychophysical vibrotactile thresholds (range 25 - 400 Hz) were determined across the unloaded sole in young and elderly subjects. Thresholds were lower in the ball and arch of the sole, than in the heel and toe regions. Elderly subjects demonstrated significantly elevated thresholds for high-frequency vibration. Secondly, microneurographic recordings were made from skin afferents of the unloaded sole in young subjects. Results indicated that while similar types of cutaneous receptors exist in the sole of the foot and hand, there appear to be differences in receptor density and distribution. Our results demonstrate that cutaneous afferent inputs from the foot sole provide useful information for the control of posture and locomotion.

INTRODUCTION

The task of maintaining an upright standing posture in the human involves a complex sensorimotor control system, with somatosensory, vestibular, and visual sensory information all contributing to the control of stance and locomotion (Inglis et al., 1994). While there is little doubt that it is the successful integration of all these inputs that leads to optimal balance control in standing, it has been suggested that somatosensory information from the lower limb appears to play a rather dominant role (Inglis et al., 1994; Fitzpatrick et al., 1994). The exact source of this essential somatosensory information remains to be determined, but recent evidence is accumulating that the glabrous cutaneous receptors from the foot sole may contribute significantly.

A number of different lines of research support this notion. Cooling of the sole of the foot, thereby reducing the input of the cutaneous information from the sole, is associated with an increase in postural sway during quiet stance (Orma, 1957; Asai et al., 1992).

* School of Human Kinetics, The University of British Columbia, Vancouver, British Columbia, Canada. Email: tinglis@interchange.ubc.ca

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Postural sway induced following galvanic vestibular stimulation (Magnusson et al., 1990b) is likewise increased following foot sole cooling. Finally, compensatory stepping reactions following a sudden postural perturbation (i.e. movement of the supporting surface) are also dramatically affected by reduced plantar support information (Perry et al., 2000).

While reduction of cutaneous foot sole information is associated with postural instability, low amplitude vibratory activation (0.2-0.5 mm, 20-80 Hz) of foot sole cutaneous afferents leads to directionally specific postural sway (Kavounoudias et al. 1998, 1999). For example, bilateral vibration of the metatarsal footpads caused sway in a backward direction. Interestingly, the velocity of the induced postural sway depended on the frequency of the vibratory stimulation, with larger velocities of sway following higher frequencies of skin vibration. Recent work by Mergner and colleges has also found that mechanical stimulation of the plantar skin, in the range of natural postural sway (i.e. 0.1-0.4 Hz), evokes sway that is highly correlated with the cutaneous stimuli (Maurer et al., 2001).

While the above studies illustrate the importance of cutaneous information in the control of standing balance, our knowledge of the nature and type of information that is available from the foot sole is largely based on indirect evidence. It seems logical that cutaneous afferents from the foot sole could code for changes in foot pressure by acting as a pressure "map". This map could monitor, much like a sensory array, the pressure changes encountered with movements of the center of presşure across the foot sole during either stance or locomotion. A few studies that have investigated vibrotactile psychophysical thresholds for the plantar skin (Kekoni et al., 1989; Nurse and Nigg, 1999) have found evidence of regional differences across the foot sole, hinting that such a map may exist. However, to assess further the role of cutaneous mechanoreceptors in bipedal stance it seems essential to understand the distribution and behaviour of the sensory receptors of the plantar skin in humans. Microneurographic recordings of cutaneous afferents from the peripheral nerves have provided direct analysis of the functional properties of skin receptors in response to various stimuli (Johansson and Vallbo, 1983; Edin, 2001). However, there are only a limited number of microneurography based studies related to the lower limb, and these have examined the hairy skin of the calf and the glabrous skin isolated to the lateral border of the foot (Vallbo & Hagbarth, 1968; Ribot et al., 1989; Edin, 2001; Trulsson, 2001). Consequently, there is no information about the characteristics of the mechanoreceptors specific to the total foot sole, their distributions, regional variations or densities, or their response characteristics.

To understand the potential contribution of plantar cutaneous afferents, and to see if this region could potentially code for information useful for postural control, two directions of research were undertaken. In the first experiment, psychophysical vibration thresholds from 55 sites across the foot sole were determined using a range of different vibrational frequencies to evaluate the nature of the regional variations in sensitivity and to establish if evidence exists for a foot sole sensor map. As a second aspect of this experiment, both young and elderly subjects were investigated, since vibrotactile thresholds are known to become elevated with aging, and this may be related to some of the postural disturbances and tendency toward increased falling in the older population. In a second experiment, microneurographic recordings were made from isolated cutaneous afferents that originated in the glabrous skin of the foot sole, in an attempt to

clarify what types of receptors are found in the foot sole, their distributions, the level of their physiological activation thresholds, and the nature of their receptive fields.

METHOD

A total of 12 subjects volunteered for the first experiment (6 young; mean age = 26 years; 6 older; mean age = 89 years). For the second experiment, 31 microneurographic recording sessions were performed (mean age 30 years). For all experiments subjects were prone lying with their right foot supported with the ankle in neutral and the foot sole surface unloaded. The clinical ethics board at the University of British Columbia approved the following experimental procedures.

For experiment 1, the vibrotactile stimulus (1.5 mm diameter cylindrical probe attached to a DC motor) was applied to the sole at 55 locations equally distributed about the foot sole (see Fig. 1). The method of limits was used to determine the psychophysical thresholds at each of 4 frequencies (25, 50, 250, and 400 Hz) and at each location. The thresholds were determined using the up and down staircase method, with the last 8 of 10 up and down pairs determining each threshold value. Stimuli were presented for 1s bursts of signal, followed by a 1 s silent period, with the amplitude of the sine wave increasing in 0.025μm steps. Amplitude was increased until the participant closed a hand switch indicating that they had felt the stimulus. To start the down portion of the staircase, the amplitude of the first stimulus burst was set to 1.5 the amplitude of the threshold amplitude from the previous up portion of the staircase. The 55 sites were tested in serial order, however order was counterbalanced between subjects to eliminate serial effects. All 4 frequencies were tested at one site before moving to a new site. Trials were blocked by frequency, however the order of presentation of the 4 blocks was randomized.

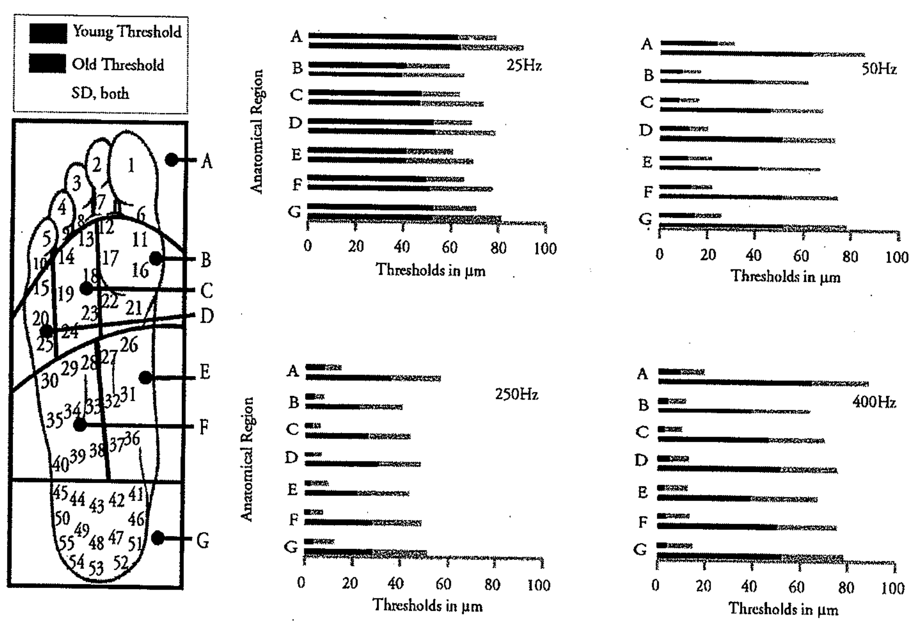

Figure 1. *Left*, an outline of the foot-sole showing the 55 points where vibration thresholds were tested, and the 7 anatomical regions into which the points were segregated. *Right*, plots showing the relationship between anatomical region (x-axis) and vibrotactile threshold (y-axis) in young and old subjects at 4 different frequencies. Thresholds were measured in μm.

For experiment 2, a sterile insulated tungsten microelectrode (0.2 mm diameter, 65-mm length, impedance 50-360 [mean 150] kΩ at 1 kHz in situ) was inserted manually into the tibial nerve at the level of the popliteal fossa. A subcutaneous electrode of similar make, placed approximately 10 mm proximally, served as a reference. By manually manipulating the recording electrode, single unit activity from low-threshold cutaneous afferents originating in the glabrous skin of the foot sole were isolated. The neurogram was amplified 10-25K and band-passed filtered between 0.3 and 10 KHz, and then analogue-to-digitally converted at a sample rate of 25-50 KHz (1401-Micro interface). Single-unit morphology was determined on-line using an oscilloscope, and verified off-line using Spike2 software (Inglis et al., 1996). Physiological threshold and receptive field sizes were determined and afferents were classified using Semmes-Weinstein monofilaments (Stoelting Co, USA) in the range of 0.5 to 5000 mN of force. A monofilament of 4-5 times threshold force was used to outline the receptive fields. Afferents were classified using the same method as previously documented (Johansson and Vallbo, 1983) into either slowly or rapidly adapting receptors and then subclassified into type I and type II afferents as follows: Slowly adapting type I (SAI); Slowly adapting type II (SAII); Fast adapting type I (FAI) Fast adapting type II (FAII)

RESULTS

To facilitate analysis of the many different regions, and so comparisons could be made with earlier reports (Kekoni et al., 1989) the 55 locations were initially grouped into 7 anatomical areas: toes, medial ball, mid-ball, lateral ball, medial arch, lateral arch and heel, and overall means and standard deviations for each sub-region were calculated for comparison. Also, grand mean thresholds (all 55 regions) were calculated separately for each frequency and age group. Figure 1 shows that the ordinal pattern of threshold level amongst the regions is age and frequency invariant. The highest thresholds were in the toes (A), followed by the heel (G) and lateral ball (D); lateral arch (F); mid-ball (C); medial arch (E); and medial ball (B). This pattern appeared to remain throughout each of the four frequencies. However, the overall pattern did seem to be different depending on age and frequency. For grand overall means, at 25 Hz, thresholds for young and old subjects were not statistically different from each other (y=40.4 μm, O=49.6 μm). At 50 Hz, thresholds decreased significantly for the younger group (13.1μm), but not for the older group (49.2 μm). At 250 Hz, both age groups exhibited their lowest thresholds, however younger thresholds (3.6 μm) were significantly lower than older thresholds (27.8 μm). At 400Hz, the thresholds for the younger subjects stayed low (4.4 μm), while the elderly thresholds increased (49.1 μm) to a similar level to what they were at 250 Hz. Regional differences demonstrated that for both young and old, the ball and the arch of the foot had lower thresholds than the heel and toes. These regional differences suggested that perhaps there is potentially a variation in innervation profiles for the different regions of the foot, suggestive of the existence of a sensory map, with a change in these profiles with aging.

In experiment 2, 106 foot sole cutaneous afferents were classified according to their type, physiological threshold, and receptive field. Based on previously established criteria (Johansson and Vallbo, 1983), there were 15 SAIs, 16 SAIIs, 60 FAIs, and 15 FAIIs. The receptors had increased activation thresholds, larger receptive

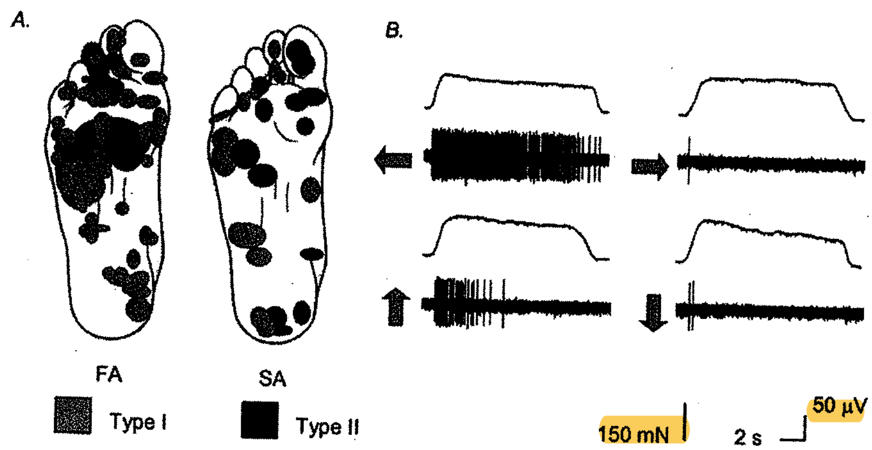

Figure 2. *A*, the positions and sizes of the receptive fields for each receptor type on the foot sole are shown above. *B*, Directional sensitivity of a SAII receptor was measured in response to repeatable skin stretch. The direction of skin stretch on the foot sole is represented by the arrow. The arrow pointing to the left indicates that the direction of stretch was toward the lateral border of the foot sole. The level of stretch applied to the skin and the accompanying discharge activity are illustrated.

field profiles, and clearly a different distribution pattern than that observed in the human hand (Johansson and Vallbo, 1983). Instead of the concentration of type I receptors in the distal phalangeal regions, the slowly adapting receptors appeared to be located more along the borders of the foot, with the fast adapting receptors having a more random distribution throughout the sole. Of note, none of the slowly adapting receptors demonstrated a background discharge. Interestingly, most of the SA II receptors did demonstrated a dramatic directional skin stretch sensitivity, as illustrated in Figure 2B by a SAII's response to 4 different directions of skin stretch.

DISCUSSION AND CONCLUDING REMARKS

Results from the psychophysical experiments show clearly that there is a regional variation in vibrotactile threshold across the human foot sole, and that these regional differences do not seem to be frequency dependent. Surprisingly, for the sole, the toe region demonstrated the highest regional thresholds, in contrast to the hand where the fingers have been shown to have the lowest regional threshold (Johansson and Vallbo, 1983). This regional variation was the same in the sole of the older subjects, but the actual thresholds for high frequency stimulation were dramatically elevated as compared to younger subjects. It seems possible that the regional variations could be due to different receptor densities, and/or different receptor physiological thresholds, within the regions of the sole. It is also possible that with normal aging there is a loss of the rapidly adapting receptors, or perhaps a change in their coding behaviour, that is responsible for the decreased ability to sense higher frequency vibrations.

The microneurographic experiments demonstrated that these regional variations are more than likely not dependent on receptor density differences across regions. There was no evidence of a regional variation in receptor density or of a decreased concentration of type I receptors in the toes, suggesting that the psychophysical variations were not due to a sensor map that is dependent on receptor concentrations. However, since both the physiological thresholds and the receptive field sizes were much larger in the sole than has been described for the hand, it is possible that the regional variations are due to the response characteristics of the individual receptors rather than their distributions. Variations between the younger and older subjects likewise could be due to this, or to variations in the skin stiffness or its mechanical behaviour changing with aging.

The results of both experiments demonstrate that the foot sole receptors can provide rich tactile information, and that this information is probably regionally specific. Issues for future study will need to include microneurographic recordings of afferents in young and elderly subjects, under different conditions of foot sole loading.

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